ANTHECOLOGY AND EVOLUTIONARY CONSIDERATIONS OF *LEONOTIS NEPETAEFOLIA* R. BR.[1]

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Leonotis nepetaefolia R.Br. flowers with anthers dehiscing in bud stage produced inflorescence on the verticillaster every day. The flowers are capable of reproducing through autogamy, geitonogamy and xenogamy, but autogamy is the predominant mode and is successful even in the total absence of an extraneous agency. The animal visitors, avians – *Nectarinia zeylanica*, *N. asiatica*, a bee *Trigona* sp. are the regular pollinators. Butterflies, which are occasional visitors, seldom act as pollinators.

From the evolutionary point of view, the flowers of *L. nepetaefolia* with their scarlet colour, degenerated lower corolla lip, predominant autogamy, higher pollen–ovule ratio and greater amounts of nectar, are suggestive of the autogamous race now occurring in India as descended from a xenogamous race.

INTRODUCTION

Cruden (1976) gave a brief account of the evolution of the weed *Leonotis nepetaefolia* R.Br., suggesting that the flower–form now occurring in India, Southeast Asia, Indonesia, Australia etc. has undoubtedly descended from a xenogamous – bird pollinated race. Except for this, the information on the flower biology and the pollination dynamics of *L. nepetaefolia* is not known. The purpose of the present study was to provide information on the anthecology and detail evolutionary considerations of *L. nepetaefolia* R.Br.

MATERIAL AND METHODS

The herb *Leonotis nepetaefolia* R.Br. (*Phlomis nepetaefolia* L.) growing wild abundantly in waste places, open forests, banks of irrigation canals, and along roadsides at Turimella (15°10'N, 81°45'E), Prakasam District, Andhra Pradesh, India, was chosen for the study. The blooming phenological events at inflorescence and flower level were observed in detail. The inflorescence flowering life span was obtained after tagging ten randomly chosen inflorescences about to initiate bloom and followed every day until they ceased to flower. Concurrently, the flower morphological characters were also observed. Following the methods of Raju (1987), Horborne (1973), Baker and Baker (1973), pollen production per flower and pollen–ovule ratios, pollen viability, stigma receptivity, recording the flower life time, nectar monitoring and analysis and breeding systems were investigated.

Representative specimens of the butterfly visitors were caught, killed, preserved and identified with Wynter Blyth (1957) and Varshney (1983); the insect species by a comparison with the identified specimens (by CIE, London) and the avian species by visual examination from close quarters, and using binoculars, and identified with Salim Ali's books. The activity period of the foragers, type of forage, behaviour at flower, share in the pollination play etc. was also observed.

RESULTS

Vegetative and Flowering phenology: Vegetative growth of *L. nepetaefolia* appears in September; flowering commences from mid—October and continues up to December/mid—January; thereafter the plants dry up.

The verticillaster inflorescence bears three verticils, each with an average of 162 flowers in the basal whorl, 188 in the second and 137 in the third

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whorl, producing over 63 days. The flowers are produced every day but each verticil does not flower successively.

Flower morphology: The floral parts show size difference in the first and the last formed flowers. The sessile flower is scarlet and gullet–shaped. Calyx tubular, ten–ribbed, green and hairy. Corolla is 2–lipped, tubular – the seat for the nectar produced at the base of ovary; upper lip is long, concave with a villous crown and lower lip small, 3–lobed and is poorly developed and non–functional. Stamens are 4, epipetalous, didynamous, housed inside the upper corolla lip, filaments hairy and hold the stamens together. Gynoecium is bicarpellary, tetralocular, syncarpous superior ovary with gynobasic style; stigma bifid—unequal lobes and situated below the stamen position.

Floral dynamics: Flower opening is accomplished every day over a short period during 2200 to 0200 hrs. The same schedule was evident on different weather days. Anthers open 20–30 minutes ahead of anthesis. Pollen gradually drops off from the anther onto the stigma geotropically in small clumps. Pollen output per flower came to be 10412 (X); they are spheroidal, 44 mm, surface smooth and cytoplasm granular, and are viable for 44 hours of anther dehiscence. Pollen–ovule ratio is 2603:1. Stigmas are receptive after anthesis and remain so for 37 hours, then corolla with stamens and stigma drops off. Calyx persists and shelters the developing seeds in it. Nectar production began two hours before anthesis and ended at

TABLE 1
FLOWER VISITORS ON *Leonotis nepetaefolia;* FORAGE TYPE AND BODY PARTS OF POLLEN DEPOSIT

Flower visitors species	Forage type	Pollen deposit region
Hymenoptera		
Apidae		
Trigona sp.	Pollen	Ventral side, legs, head
Formicidae		
Camponotus sericeus	Nectar	-do-
Lepidoptera		
Danaidae		
Danaus chrysippus	-do-	Proboscis
Euploea core	-do-	-do-
Pieridae		
Catopsilia crocale pomona		
C. pyranthe	-do-	-do-
Papilionidae		
Polydorus aristolochiae	-do-	-do-
Nymphalidae		
Hypolimnas misippus	-do-	-do-
Thysanoptera		
Thripidae		
Thrips hawaiiensis	-do-	Entire body
Nectariniidae		
Nectarinia asiatica	-do-	Bill, Forehead
N. zeylanica	-do-	-do-

0800 hrs, the corolla tube gets filled; amount produced was 6 ml/flower. Sugar concentration is 18% and composed of glucose, sucrose and fructose (Gsf); amino acids and proteins are also found.

Breeding behaviour: Hand–pollination done to test the various modes of reproduction showed that apomixis is totally lacking, reproduction is by autogamy (100%), geitonogamy (100%) and xenogamy (48% fruit set; 62% seed set; 30% fecundity). Open pollinations also yielded 100% in fruit set and seed set as well as in fecundity.

Flower visitors' activity: A total of ten species was recorded at the flowers– two avian species of Nectariniidae, two hymenopterans (bee and ant) and six lepidopterans. Besides these, thrips are also found in the flowers. All these are day—active: sunbirds and ants during 0600–1800 hrs, *Trigona* sp. during 1100–1500 hrs, and the butterflies during 1000–1600 hrs.

Only avian species are consistent and frequent visitors throughout the season. Sunbirds, ants and butterflies visited the flowers for nectar. They emptied the flower in a single visit. The stingless bee *Trigona* sp. visited the flowers for pollen only (Table 1). *Trigona* sits against the stamens and moves onto the anthers and collects pollen; then the stigma and stamens are forced out of the upper corolla lip. Consequently, the pollen falls on the stigma in small clumps and the ventral side of the bee's body brushes against the reproductive parts. *Camponotus sericeus* do not disturb the flower and take nectar from lateral side. The butterflies approach the flower laterally and from the front, to obtain nectar; the reproductive parts come into contact with the proboscis when the butterfly approaches from the front. However, all the visits are not successful.

The sunbirds behave at the flower in two ways: a) they sit at the inflorescence axis, insert the bill into the flower of the side of inflorescence from the front; b) they sit at the inter—verticil region of the inflorescence, and insert the bill into the flower tube from above, through the corolla lip; then the lip is ruptured vertically in the centre. In either case, the stigma and stamens come out of the hooded lip but without any damage to the reproductive parts. The manner of pollen fall on the stigma was the same as occurred when *Trigona* sp. foraged. Two plant species *Anisomeles malabarica* and *A. indica* compete with *Leonotis nepetaefolia* for pollinator service, especially from avian species.

Discussion

Pollination: The flowers are visited by the avian *Nectarinia* sp., the stingless bee *Trigona* sp., the ant *Camponotus sericeus* and butterflies. The sunbirds may reach the nectar either by inserting the bill in the legitimate way (Fig. 1a) or by piercing the upper corolla lip from above, making a vertical slit in the mid—part of the corolla (Fig. 1b). *Trigona* sp. collects pollen sternotribically and the butterflies suck the nectar and seldom effect pollination. The ants forage on nectar and do not establish contact with the stigma and pollen and hence act as nectar robbers. *Trigona* sp. and butterflies are not regular visitors. The birds are regular and consistent and their visits to the flowers force the essential organs out of the upper corolla lip and obtain nectar nototribically, while it is sternotribic for *Trigona* sp. and is seen heavily dusted with pollen upon visiting the flower. The plants reproduce through autogamy, geitonogamy and xenogamy –the first as superior. Controlled pollinations of autogamy indicated 100% success in fruit set and fecundity even in the total absence of flower visitors. When visitors are absent, the pollen, after getting dried, drops onto the stigma, resulting in auto–pollination.

Structurally, the flowers are gullet–blossoms, the stigma and anthers are hidden inside the woolly upper corolla lip; anthers dehisce by longitudinal slits, nectar is abundant, dilute and is well suited for the sunbirds to sip. The lower corolla lip is not well developed and shrivels away soon after anthesis. The sunbirds showed a preference for scarlet *L. nepetaefolia* flowers, when *Anisomeles indica, A. malabarica* (blue flowers) were available at a place, thus suggesting a preference for scarlet flowers. Evidently, *L. nepetaefolia* does not rely on pollinator activity

for its reproduction, but certainly such activity may contribute to xenogamy and the resultant genetic variability.

Salim Ali (1932) has compiled a list of plant species pollinated by sunbirds and by others, where members of Lamiaceae such as *Salvia splendens* and *L. nepetaefolia* are given as visited by sunbirds. The present study adds *Anisomeles* sp. to such a list. The *Anisomeles* sp. are not only visited for nectar but are pollinated in their act of foraging.

The sunbirds are known to exhibit site specificity and it seems to be maintained over a long period of time. In certain cases, they probe the flowers in an illegitimate way and sip the nectar (Salim Ali 1932). In the present study, the sunbirds were seen occupying nests in the nearby bushes of *Euphorbia antiquorum* or other plant species and regularly paid visits to a particular patch of *Anisomeles* or *L. nepetaefolia*. The pollination by sunbirds at the study area was not dense, hence there was no competition for floral resource. The sunbirds approached the flowers of *Anisomeles* sp. in the legitimate way, but they usually punctured the corollas of *Leonotis nepetaefolia*.

Nectar and pollen–ovule ratio: Heinrich (1975) discussed that the flowers to be pollinated by large bodied animals requiring high energy produce significantly more nectar compared to the flowers pollinated by small—bodied low energy requiring organisms; and most of the outcrossed plants produce relatively large amounts of nectar. Contrary to this, the autogamous *L. nepetaefolia* produced more of diluted nectar similar to that of bird–flowers. The pollen–ovule ratios are also greater as in xenogamous flowers in contrast to the prediction of Cruden (1977) that autogamous species will have lower P/O's than xenogamous flowers. Presumably, the *L. nepetaefolia* autogamous race occurring in India might have descended from a xenogamous bird–pollinated race as suggested by Cruden (1976), but the degeneration of breeding system is not accompanied by a similar degeneration of other floral characters as corolla colour, pollen–ovule ratio and nectar production.

Cruden (1976) suggested the possible lines of evolution of breeding system in *Leonotis nepetaefolia* on the basis of his observations on the populations in the New World. He found the small flowered form as well as the large flowered form and a third form occurring in eastern Africa which has given rise to the weedy populations in southeast Asia, Indonesia, Australia etc. The small flowered form is facultatively xenogamous and is pollinated by hummingbirds and small bees. The large flowered form is xenogamous and is pollinated in Kenya by sunbirds (Gill and Wolf 1975), but in the New World it is visited illegitimately by hummingbirds which take nectar from the flowers by slitting the corolla or depressing it from above. He further states that the large flowered form is recently arrived in the New World and that the evolution of an autogamous race may be occurring. Therefore, it is likely that the form now studied might have originated from a xenogamous race.

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